Migratory connectivity of a Neotropical migratory songbird revealed by archival light-level geolocators

MICHAEL T. HALLWORTH,[1,2,5] T. SCOTT SILLETT,[1] STEVEN L. VAN WILGENBURG,[3,4] KEITH A. HOBSON,[3]
AND PETER P. MARRA[1]

[1]*Migratory Bird Center, Smithsonian Conservation Biology Institute, National Zoological Park, MRC 5503, Washington,
D.C. 20013 USA*
[2]*College of Science, George Mason University, 4100 Patriot Drive, Fairfax, Virginia 22030 USA*
[3]*Environment Canada, 11 Innovation Boulevard, Saskatoon, Saskatchewan S7N 3H5 Canada*
[4]*Environment Canada, 115 Perimeter Road, Saskatoon, Saskatchewan S7N 0X4 Canada*

Abstract. Understanding migratory connectivity is critical for interpreting population dynamics, seasonal interactions, and for the implementation of conservation strategies of migratory species. We evaluated the migratory connectivity of a Neotropical migratory songbird, the Ovenbird (*Seiurus aurocapilla*) using archival light-level geolocators deployed at two breeding and four nonbreeding locations while incorporating Ovenbird abundance as prior information using Bayes' Rule. We also included band recoveries submitted to the United States Geological Survey's Bird Banding Laboratory to assess connectivity of areas where geolocators were not deployed. We created a probabilistic map of origin for each capture site and mapped spring migration routes between nonbreeding and breeding locations. We found a complete separation of eastern and western populations of Ovenbirds throughout the annual cycle. Breeding Ovenbirds from western Canada spent the nonbreeding season throughout Central America and migrated through central North America during spring migration. Birds breeding in the northeastern United States were distributed throughout the central Greater Antilles in the Caribbean and migrated through eastern North America during spring migration. Fall migration routes were not included because the timing of migration coincided with fall equinox when latitudinal estimates are unreliable. However, longitudinal estimates suggest no overlap between eastern and western populations during fall migration. Ovenbirds with geolocators attached in Jamaica bred in the northeastern United States with the highest posterior probability of origin found in Massachusetts, while Ovenbirds captured in Florida and Puerto Rico bred primarily in the mid-Atlantic. Incorporating Ovenbird abundance as a prior into geolocator estimates decreased the area of origin by 90.37% ± 1.05% (mean ± SE) for the breeding season and 62.30% ± 1.69% for the nonbreeding season, compared to geolocator estimates alone. Ovenbirds exhibited strong migratory connectivity between breeding and nonbreeding season, which has important implications for various aspects of the ecology, evolution, and conservation.

*Key words: Bayesian; Caribbean basin; conservation biogeography; geo-logger; migration; movement ecology; Ovenbird (*Seiurus aurocapilla*); probability of origin; spatial distribution.*

INTRODUCTION

Elucidating patterns of migratory connectivity, the degree to which breeding and nonbreeding populations of migratory species are geographically linked, is essential for advancing our understanding of most facets of the ecology and evolution of these species as well as for prioritizing conservation efforts (Webster et al. 2002, Marra et al. 2006, 2011). Identifying the strength of migratory connectivity has been especially difficult for small migratory organisms such as songbirds because of the geographic scales over which they occur annually and because their small size

generally precluded the attachment of tracking devices.

The miniaturization of archival light-level geolocators (hereafter geolocators) has facilitated the tracking of individual songbirds as they move between breeding and nonbreeding locations (Stutchbury et al. 2009, Ryder et al. 2011, Laughlin et al. 2013, Renfrew et al. 2013). Geolocators provide temporally and spatially explicit estimates of geographical location that include approximate latitudinal and longitudinal coordinates. Geographic locations can be determined from archived light intensity levels to estimate sunrise and sunset times and thereby calculate day length and the time of midday, giving latitude and longitude, respectively (Hill 1994). Although geolocators have drawbacks, including cost, the need to recapture individuals, often low recovery

rates related to potential effects on survival and behavior (Arlt et al. 2013, Costantini and Møller 2013, Gómez et al. 2013), and uncertainty in assigning light transition events to latitude and longitude (Lisovski et al. 2012), geolocators have increased our understanding of migratory connectivity for several species (e.g., Stutchbury et al. 2009, Heckscher et al. 2011, Ryder et al. 2011, Stanley et al. 2012, Contina et al. 2013, Renfrew et al. 2013).

Because individual tracking methods like geolocators only provide information on individuals initially marked, they must be deployed in multiple locations throughout a species' range to gain a broader understanding of migratory connectivity. The majority of geolocator studies have thus far been conducted during the breeding season (Stutchbury et al. 2009, Heckscher et al. 2011, Ryder et al. 2011) and usually at a small number of deployment locations limited to only a small portion of a species range. With few exceptions (Stanley et al. 2012, McKinnon et al. 2013), our understanding of migratory connectivity results from few deployment locations during breeding season. The strength of migratory connectivity may differ between populations throughout a species range. Thus, conclusions of migratory connectivity drawn from a single deployment location may be misleading. Therefore, multiple deployment locations throughout a species range are needed to determine the strength of migratory connectivity.

Here, we examine the migratory connectivity of a small (~18 g) passerine, the Ovenbird (*Seiurus aurocapilla*), throughout its breeding and nonbreeding range. Ovenbirds are a widely distributed species in both the breeding and nonbreeding seasons and are capable of carrying geolocators throughout the annual cycle (Hallworth et al. 2013), making them an ideal species for quantifying migratory connectivity. We deployed geolocators at two widely separated (>2700 km) locations during the breeding season and four locations throughout the nonbreeding range to determine the strength of migratory connectivity. We predicted that breeding populations of Ovenbirds in eastern and western North America would correspondingly spend the nonbreeding season in the eastern and western parts of their nonbreeding range. Similarly, we predicted that Ovenbirds captured in eastern, central, and western portions of the Caribbean basin would breed in eastern, central, and western North America and migrate through eastern, central, and midwestern North America, respectively. We also predicted that Ovenbirds captured in the northern portion of their nonbreeding distribution would breed further south than birds captured in the southern extent of their nonbreeding distribution, consistent with leap-frog migration (Newton 2008, Langin et al. 2009).

METHODS

Breeding season fieldwork was conducted at the Hubbard Brook Experimental Forest (HBEF), New Hampshire, USA (43.93° N, 71.93° W) and Prince Albert National Park, Saskatchewan, Canada (53.89° N, 106.16° W). During the nonbreeding season, we conducted field work in Everglades National Park, Florida, USA (25.13° N, 80.94° W), Guanica Dry Forest, Puerto Rico (17.97° N, 66.87° W), Fonthill Nature Preserve, St. Elizabeth Parish, Jamaica (18.04° N, 77.94° W), and at the Belize Foundation for Education and the Environment, Toledo District, Belize (16.55° N, 88.69° W). At two breeding and four nonbreeding locations, Ovenbirds were captured using simulated territorial intrusions and passive mist-netting techniques (Faaborg and Arendt 1984). We attached geolocators (British Antarctic Survey, Models MK12 [1.0 g] and MK20SALT [0.9 g]) to individuals >19.0 g with a leg harness technique (Naef-Daenzer 2007). We deployed 51 on birds breeding at HBEF in 2010 (*n* = 17 birds) and 2011 (*n* = 34 birds) and 46 on birds breeding at Prince Albert National Park, Canada in 2011. Eighteen geolocators were attached to Ovenbirds in Everglades National Park, Florida, USA, during the 2010–2011 nonbreeding season. Twenty-eight geolocators were deployed during the 2009–2010 (*n* = 11 birds) and 2010–2011 (*n* = 17 birds) nonbreeding seasons in Jamaica, while 18 and 21 were attached in Puerto Rico and Belize, respectively, during the 2011–2012 nonbreeding season. We attempted to recapture these individuals during the subsequent year to retrieve the geolocators (Fig. 1).

Light-level interpretation

Sun elevation calibration.—Light data were transformed into estimated positions (latitude and longitude) using BASTRACK version 19.0 (British Antarctic Survey, Cambridge, UK). Transitions were determined using TRANSEDIT (British Antarctic Survey) with a threshold value of 5. We set the minimum dark period to 4 hours and removed any transitions that were less than 4 hours apart; transition data were used to determine the sun elevation angle associated with a light threshold of 5 at the different capture locations (Appendix: Table A1). Light-transition events can be affected by several factors such as weather, topography, and habitat (Lisovski et al. 2012). Because these factors differ during the phases of the annual cycle, we used sun elevation angles to determine individual locations that correspond with breeding and nonbreeding seasons. To ensure that the sun elevation angle was representative of the capture location, only transitions that occurred while at the capture site were used. The breeding season sun elevation angle was determined using transition events that occurred during the stationary period at a known capture site (deployment date to 31 July and arrival date [if known or 1 June if unknown] to recapture date). Similarly, the nonbreeding season sun elevation angle was determined using transitions that occurred while at the capture location in the tropics (deployment date to 31 March and 1 December to the recapture date). Once the sun elevation angles were identified for the breeding
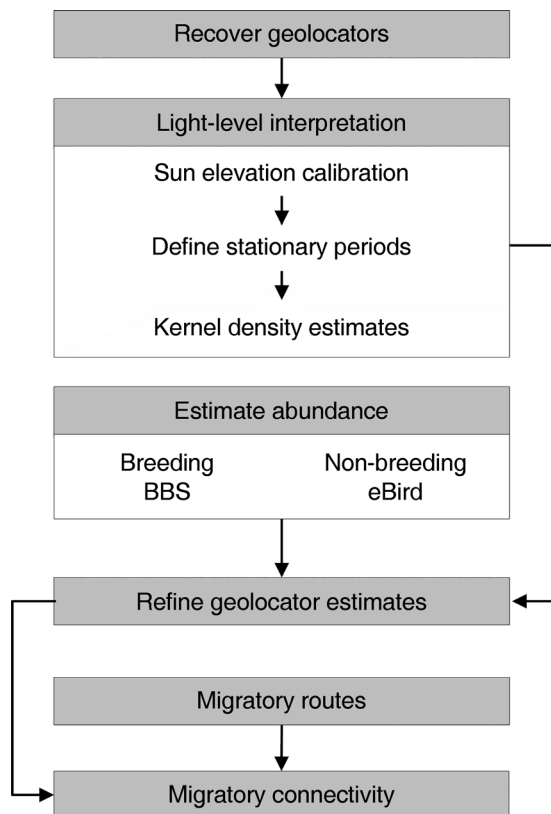
Fig. 1. Schematic illustrating the process for deriving and refining location estimates from archival light-level geolocators using bird abundance. Geolocator estimates refined using bird abundance were used to determine the strength of migratory connectivity for Ovenbirds. Arrows depict the workflow of the analysis.

and nonbreeding periods, we used them to determine the locations of individuals captured during different periods of the year. To determine breeding locations we used either the sun elevation angle of the capture location if individuals were captured during the breeding season (McKinnon et al. 2013) or the mean sun elevation angle for the breeding season (−1.335°) if individuals were captured during the nonbreeding season. To determine nonbreeding locations we used either we the sun elevation angle of the capture location if captured during the nonbreeding season (McKinnon et al. 2013) or we used the mean nonbreeding sun elevation angle (−3.409°) if individuals were captured during the breeding season. A third sun elevation angle was used to identify the nonbreeding location of two individuals breeding at Prince Albert National Park, Saskatchewan, because the mean nonbreeding season sun elevation angle (−3.409°) identified the nonbreeding exclusively over the Gulf of Mexico. The sun elevation angle from a reference geolocator placed near the forest floor in Belize (1.194°, Table A1) was used instead for these two Ovenbirds.

Stationary periods.—Nonbreeding locations were identified as estimated positions occurring between 1 November and 31 March. All data collected during the spring equinox (3 March–4 April) were removed because latitude is not reliably estimated during that timeframe as day length is similar everywhere. Breeding locations were identified as geolocator positions that occurred between 1 June and 31 July. The first of June was used as the start of the breeding to avoid positions obtained during migration.

Kernel density estimates.—To determine probable breeding and nonbreeding locations of individuals, we separately fit kernel density estimates (KDE) to geolocator positions for each individual. We used least-squares cross validation (LSCV) to estimate bandwidth (Gaussian smoothing parameter; Barg et al. 2005) for each KDE, which were generated using all breeding (1 June–31 July) and nonbreeding (1 November–31 March) locations. KDEs did not include locations that occurred during the period around spring equinox (3 March–4 April). Precision in geolocator estimates was similar for geolocators deployed during breeding (median, 521 506 km^2; 95% CI, 401 189–641 823 km^2) and nonbreeding (median, 565 115 km^2; 95% CI, 225 019–905 211 km^2) seasons.

Refining geolocator estimates

We further refined probable breeding and nonbreeding locations of individuals using Ovenbird abundance as prior probabilities in a Bayesian framework (Royle and Rubenstein 2004, Norris et al. 2006). We incorporated Ovenbird abundance, which assumes probable breeding and nonbreeding locations are affected only by abundance, to reduce the uncertainty of estimates associated with geolocators alone. Ovenbird abundance during the breeding (Sauer et al. 2012) or nonbreeding season (see *Nonbreeding abundance*), depending on capture location, were used as prior probabilities in Bayes' Rule

$$f(b\,|\,y) = \frac{f(y\,|\,b)f(b)}{\sum_{b=1}^{B} f(y\,|\,b)f(b)}$$

where $f(y\,|\,b)$ is the kernel density estimate determined from geolocators, $f(b)$ is the probability of being randomly drawn from the population given Ovenbird abundance, and B is the number of raster cells located within the breeding or nonbreeding distribution. The abundance of Ovenbirds was estimated from Breeding Bird Survey data (Sauer et al. 2012) for the breeding season. Currently, no range-wide monitoring data are available for the nonbreeding distribution; therefore, we used eBird checklists (Avian Knowledge Network) reported from the Ovenbirds nonbreeding range (see Ridgely et al. 2003) to determine nonbreeding abundance.

Nonbreeding abundance

We considered multiple competing models for nonbreeding abundance of Ovenbirds in which we modeled the number of Ovenbirds detected at nonbreeding

locations submitted via eBird checklists. Nonbreeding abundance maps were created from eBird checklists that reported observer effort, every species detected, provided the number of Ovenbirds detected, and were collected between 1 November and 31 March in the years 2010–2013. The number of eBird checklists submitted within the wintering distribution of Ovenbirds between 1 November and 31 March has increased exponentially since 2009 (Appendix: Fig. A1). Checklists submitted between 2010–2013 were pooled to increase the likelihood that sites were sampled multiple times between 1 November and 31 March. To maximize the amount of coverage across the nonbreeding distribution, we assumed no change in abundance between 2010 and 2013. Encounter histories were structured by month between November and March resulting in five sampling occasions at 17 103 sites. Geolocator data suggest that some individuals arrive to nonbreeding sites during the month of October and begin northward migration during April. Therefore, we excluded October and April so no individuals would enter or exit the population in order to maintain the assumption of population closure (MacKenzie et al. 2002). The total number of Ovenbirds seen at a location during the encounter intervals was used to estimate abundance. Ovenbirds were assumed to be absent if no Ovenbirds were observed and all species were reported for a particular checklist. We built our nonbreeding season abundance map using 74 838 eBird checklists from 17 103 locations submitted between 1 November and 31 March in the years 2010–2013; 1493 checklists (2%) submitted from 563 locations detected at least one Ovenbird. The mean number of Ovenbird observations per location was 1.33. Longitude, elevation, and the mean difference of Normalized Difference Vegetation Index (NDVI) between March and November of locations were used as covariates in the candidate model set (see the Appendix). We considered models with main effects and included models with up to second-order polynomial (quadratic) terms for longitude and elevation. Longitude was included in the candidate model set to test whether abundance was highest in the center of the nonbreeding distribution. Elevation was included to determine whether Ovenbird abundance changes along an elevation gradient. The difference between March and November NDVI values were included in the candidate model set as a proxy for habitat type (values <0 indicate browning, values = 0 indicates no change, values >0 indicate greening). The digital elevation model was obtained from databasin.org (*available online*).[6] Monthly NDVI values (November–March) were obtained from National Aeronautics and Space Administration's Earth Observations (NASA's NEO) website (*available online*).[7]

We modeled Ovenbird abundance from eBird checklists data by selecting among Poisson, zero-inflated Poisson, and negative-binomial N-mixture models (Royle and Dorazio 2008) to determine the distribution that best fit the data. The negative binomial distribution had the lowest Akaike information criterion (AIC) value (Appendix: Table A2) and thus the negative binomial distribution was used to model Ovenbird abundance during the nonbreeding season using N-mixture models (Royle and Dorazio 2008). Relative abundance of Ovenbirds during the nonbreeding season were modeled using the *pcount* function in the *unmarked* (Fiske and Chandler 2011) package and the predictions were mapped using the *raster* (Hijmans and van Etten 2012) package in program R (R Core Team 2013). We considered multiple competing models for nonbreeding abundance of Ovenbirds in which we modeled counts as a function of the change in NDVI, latitude, elevation, and squared terms for both elevation and latitude. In order to account for imperfect detection we selected among competing models in which detection probability was modeled as either a constant or in which the total amount of time (count minutes) and the number of checklists submitted (number counts) during each month were included as observation covariates.

Breeding abundance

Ovenbird abundance during the breeding season was obtained via the Breeding Bird Survey, which incorporated mean Ovenbird counts on survey routes from 2006 to 2010 using the start of the 39.43-km sampling route as the sampling location. Abundance was then interpolated using inverse distancing weighting to create a contour map of estimated mean abundance across the survey area (Sauer et al. 2012). Further details on how the Ovenbird breeding season abundance map was generated using Breed Bird Survey data is *available online*.[8]

Migration

Spring migration routes were estimated from the two geolocator locations generated daily from time of relative "noon" (sunrise to sunset) and "midnight" (sunset to sunrise). Only noon locations were used to determine migration routes because midnight locations may be influenced by the Ovenbird's nocturnal migratory behavior. We included all points during spring migration. However, once individuals migrated north of the Tropic of Cancer (23.5° N) we used locations derived using the breeding sun elevation angle. Prior to crossing the tropic of cancer, locations were derived using the nonbreeding sun elevation angle. Fall migration routes were not considered because the timing of fall migration for Ovenbirds corresponds with fall equinox when latitude is not reliably estimated. However, we compared longitudinal estimates during fall migration (1

September–31 October) for each capture location to determine if migratory routes in the fall overlap for individuals captured at different locations. To generate spring migration routes, we assumed that the error associated with location data was similar during both stationary and migratory periods. We incorporated longitude and latitude error into each model (Sibert et al. 2012) by estimating the error around the known capture location. We used individual error estimates for birds captured during the breeding season, and the mean error for birds captured during the nonbreeding season due to the relatively small change in day length at tropical latitudes. To determine the starting (if captured during the breeding season) or ending (if captured during the nonbreeding season) location, which were included in the model as known locations, we used the mean location of geolocator estimates weighted by the posterior probability surface created using Ovenbird abundance as prior probabilities and KDEs with Bayes' rule calculated with Spatial Analyst in ArcMap 10.0 (Esri, Redlands, California, USA). The beginning of migration was determined by longitudinal movements that exited the nonbreeding posterior probability surface. The arrival date to the breeding grounds was identified as the first location that fell within the breeding posterior probability surface (Hallworth et al. 2013). The most probable migration route and 95% confidence intervals (CI) were generated using the *kftrack* package (Sibert et al. 2012) in R version 2.15.0.

Migratory connectivity

To assess the strength of migratory connectivity, we created a probability of origin map for each breeding and nonbreeding capture location. Here, we define the probability of origin as either the nonbreeding or breeding locations of individuals captured during the breeding or nonbreeding seasons, respectively. Therefore, the probability of origin denotes either the nonbreeding locations for birds captured during the breeding season or the breeding areas for birds captured during the nonbreeding season. We depicted the probable origins for multiple individuals within a given geographic sample (e.g., HBEF, etc.) by summing the individual posterior probability surfaces and dividing by the sample size to derive a mean probability of origin map for the sample. The resulting probability of origin map is spatially explicit and depicts error associated with geolocator estimates unlike point-based measures of connectivity such as nearest neighbor (Fraser et al. 2012), graph theory (Iwamura et al. 2013), or a Mantel test (Ambrosini et al. 2009, Cormier et al. 2013). To compare the strength of migratory connectivity between capture locations, we scaled the probability of origin using

$$\frac{\Pr(\text{origin}) - 1/n}{E - 1/n}$$

where $\Pr(\text{origin})$ is the maximum posterior probability of origin when incorporating Ovenbird abundance as prior

information in a Bayesian framework, n is the number of geolocators recovered at each sample location, and E is the maximum posterior probability of origin for a known capture location. In theory, the maximum posterior probability of origin should be equal to 1, however because of the uncertainty associated with geolocator estimates the maximum posterior probability of origin was less than 1 (see Table 1). The resulting scaled connectivity values ranged between 0, no overlap of individual geolocator estimates, and 1, all individual geolocator estimates overlap entirely in the subsequent season. We categorized scaled migratory connectivity values between 0 to 0.333, 0.334 to 0.666, and 0.667 to 1.00 as weak, moderate, and strong migratory connectivity, respectively.

We also used band recoveries submitted to the United States Geological Survey's Bird Banding Laboratory to assess migratory connectivity of Ovenbirds from a broader geographic area and to include locations where geolocators were not deployed (Ryder et al. 2011). Ovenbird encounter data were obtained from the Bird Banding Laboratory and included all Ovenbird encounters up until February 2011. Ovenbirds that were banded between 1 June and 31 July and encountered between 1 November and 31 March, or banded between 1 November and 31 March and encountered between 1 June and 31 July were used to avoid individuals encountered during migration.

Results

Forty-four (24.7%) geolocators were recovered from six locations throughout the Ovenbird's breeding and nonbreeding ranges. Sixteen (18.9%) were recovered during the nonbreeding season (Jamaica, 2010 $n = 3$, 2011 $n = 6$; Everglades, 2011 $n = 3$; Puerto Rico, 2012 $n = 4$; Belize, 2012 $n = 0$), and 29 (29.8%) were recovered during the breeding season (HBEF, 2010 $n = 3$, 2011 $n = 18$; western Canada, 2011 $n = 8$). Apparent survival rates did not differ between Ovenbirds with (0.675 ± 0.06 [mean ± SE]) and without (0.549 ± 0.08) geolocators breeding at HBEF (Appendix; and data not reported). We did not attempt to relocate birds during the nonbreeding season that were captured but did not meet the mass requirement (>19.0 g) to carry a geolocator, and no birds were marked with only bands at the Canadian site. Hence, we are unable to compare survival rates of birds with and without geolocators during the nonbreeding season or for the Canadian breeding location.

Incorporating abundance

The most parsimonious model included the effect of elevation[2] and the mean difference in NDVI scores between March and November (Appendix: Table A2, Figs. A2 and A3) on Ovenbird abundance and detection probability varying as a function of total count minutes (Fig. A2). Ovenbird abundance was highest in dry, low-elevation locations. Beta estimates from the most

parsimonious model were used to create a spatially explicit Ovenbird abundance map during the nonbreeding season. This map was converted to a probability surface by dividing it's summation across the surface.

Incorporating Ovenbird abundance as a prior probability using Bayes' rule decreased the potential area of origin by 90.37% ± 1.05% (mean ± SE) during the nonbreeding and 62.30% ± 1.69% during the breeding season compared to the potential area of origin using 95% KDEs of geolocator positions alone. The area of potential origin during the nonbreeding season was reduced by 26.88% ± 1.78% even after accounting for the removal of open water encompassed by the KDE. Our Bayesian analyses also decreased the 75% and 50% KDE by 21.89% ± 4.02% and 35.28% ± 5.04%, respectively, during the nonbreeding season and by 56.50% ± 2.30% and 61.63% ± 2.89% during the breeding season.

Migration

We recovered data from 44 geolocators from five capture locations; the batteries of two (4.54%) geolocators failed during the nonbreeding season prior to migration. Individuals with geolocators captured at HBEF ($n = 20$), Everglades National Park ($n = 3$), Puerto Rico ($n = 4$), and Jamaica ($n = 9$) all migrated along the Atlantic coast during spring migration (Fig. 2). Two individuals captured in Canada migrated around the Gulf of Mexico and six flew over the Gulf, but all migrated along the Mississippi River valley before moving west toward their breeding location. Fall migration routes were not considered because fall equinox coincides with Ovenbird migration when latitude is not reliably estimated. However, longitudinal estimates are unaffected by the equinox, thus longitudinal estimates during fall migration period were compared for the different capture locations. Longitudinal estimates during fall migration suggests significant overlap for individuals captured at HBEF, Everglades National Park, Puerto Rico, and Jamaica. However, no overlap in longitudinal estimates were observed between eastern populations and individuals captured in Canada (Fig. A4).

Migratory connectivity

The strength of migratory connectivity for Ovenbirds varied between and among capture locations. Connectivity between eastern and western breeding populations were completely nonoverlapping during the nonbreeding season (Fig. 3). Individuals breeding in western Canada spent the nonbreeding season in Central America with the maximum posterior probability of origin occurring in Mexico, followed by Nicaragua, El Salvador, and Honduras. Ovenbirds breeding at HBEF spent the nonbreeding season in the Caribbean with the highest posterior probability of origin occurring in the Dominican Republic, followed by Haiti, Bahamas, Cuba, and Jamaica. In contrast, birds with geolocators attached on

nonbreeding areas exhibited overlap in breeding areas (with the exception of Jamaica). Ovenbirds captured in Everglades National Park, Florida, USA had the largest posterior probability of origin in the mid-Atlantic region of the United States, followed by the northeastern United States and southeastern Canada. Ovenbirds captured in Jamaica exhibited the largest posterior probability of origin in the northeastern United States. Individuals captured in Puerto Rico also bred along the eastern United States with the highest probability of origin found in the mid-Atlantic region followed by the northeastern United States (Fig. 3).

The scaled strength of within-population connectivity ranged from weak to moderate (Table 1). Ovenbirds captured in Jamaica exhibited the strongest connectivity (0.635) followed by HBEF (0.525), Everglades (0.360), Puerto Rico (0.336), and western Canada (0.213).

We contrasted banding encounters submitted to the Bird Banding Laboratory with geolocator data to determine migratory connectivity across a broad geographic range. A total of 252 688 Ovenbirds were banded between 1960 and 2011, 360 (<0.14%). Ovenbirds were re-encountered between 1922 and 2011. However, only three (0.001%) recapture events matched our criteria where initial capture and subsequent encounters must connect breeding and nonbreeding locations. Band recovery data appeared concordant with connectivity patterns determined by geolocators (Fig. 3).

DISCUSSION

Understanding the patterns and strengths of migratory connectivity is essential for interpreting population dynamics, life history strategies, seasonal interactions (Marra et al. 1998, Miller et al. 2012, Rockwell et al. 2012), responses to climate change (Wilson et al. 2011, Fraser et al. 2012, Iwamura et al. 2013, McKellar et al. 2013, Small-Lorenz et al. 2013) as well as the development and implementation of conservation plans for migratory species (Marra et al. 2011). To assess the strength of migratory connectivity, multiple populations throughout breeding and nonbreeding distributions need to be tracked. Our results suggest that Ovenbirds exhibit a strong east-west separation. However, individuals breeding within the eastern and western portions of the species' breeding range overwinter in different regions in the Caribbean and Central America, respectively.

Patterns of migratory connectivity can be influenced by a variety of factors acting throughout the annual cycle. Barriers to migration such as mountain ranges (Delmore et al. 2012), inhospitable environments (i.e., deserts), and large bodies of water (Tøttrup et al. 2008, 2012, Åkesson et al. 2012) may all influence the patterns of migratory connectivity. Here, we found that Ovenbirds breeding at the Hubbard Brook Experimental Forest, New Hampshire, spent the nonbreeding season exclusively in the Caribbean Basin, while birds breeding
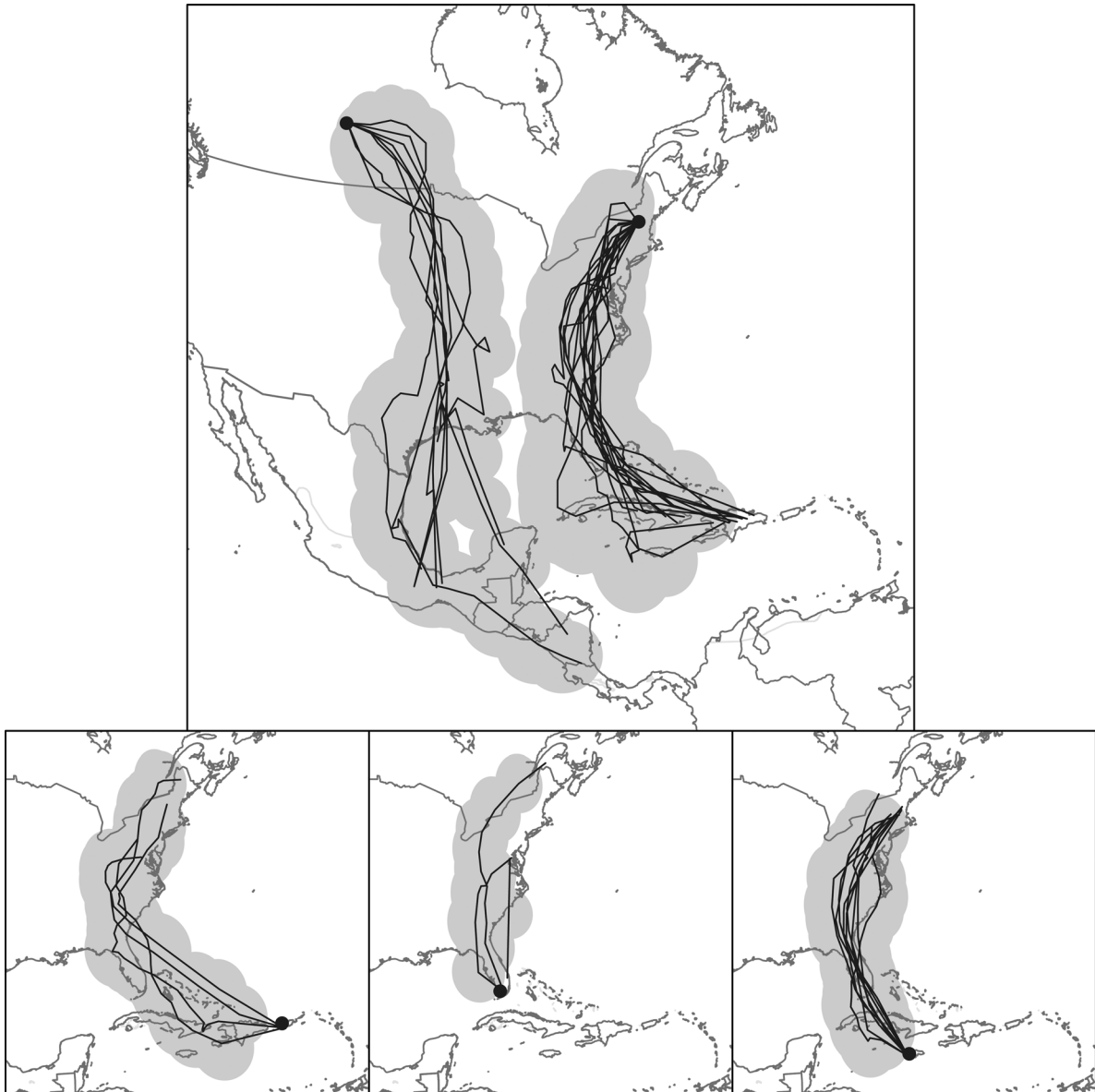
Fig. 2.   The most probable spring migration routes (lines) and 95% confidence intervals (shaded area) of Ovenbirds ($n = 43$ birds) captured at five locations across a broad geographic distribution determined using "noon" locations obtained with archival light-level geolocators. Capture locations are illustrated with dots. Fall migration was not considered because the Ovenbird migration overlaps with the fall equinox when latitudinal location estimates are not reliable.

in western Canada spent the nonbreeding season in Central America. Our results suggest that the segregation between breeding populations using the Caribbean Basin vs. Central America may occur along the Mississippi River valley. Genetic analysis of other Neotropical migratory songbirds has revealed strong segregation between eastern and western breeding populations along the Rocky Mountains (e.g., Clegg et al. 2003, Boulet et al. 2006, Irwin et al. 2011, Rundel et al. 2013). Our findings also suggest segregation between eastern and western populations although the split is east of the Rocky Mountains and may result from more

subtle barriers within different migratory flyways. Spring migration routes and longitudinal estimates during fall migration suggest that eastern and western populations migrate along different non-overlapping migratory flyways, which may have led to the broad-scale migratory connectivity separation exhibited by Ovenbirds. In addition, the strength of migratory connectivity was higher within than between the flyways, further supporting migratory flyways contribute to broad-scale connectivity patterns.

Other studies demonstrate that migratory songbirds from within the same breeding population go to
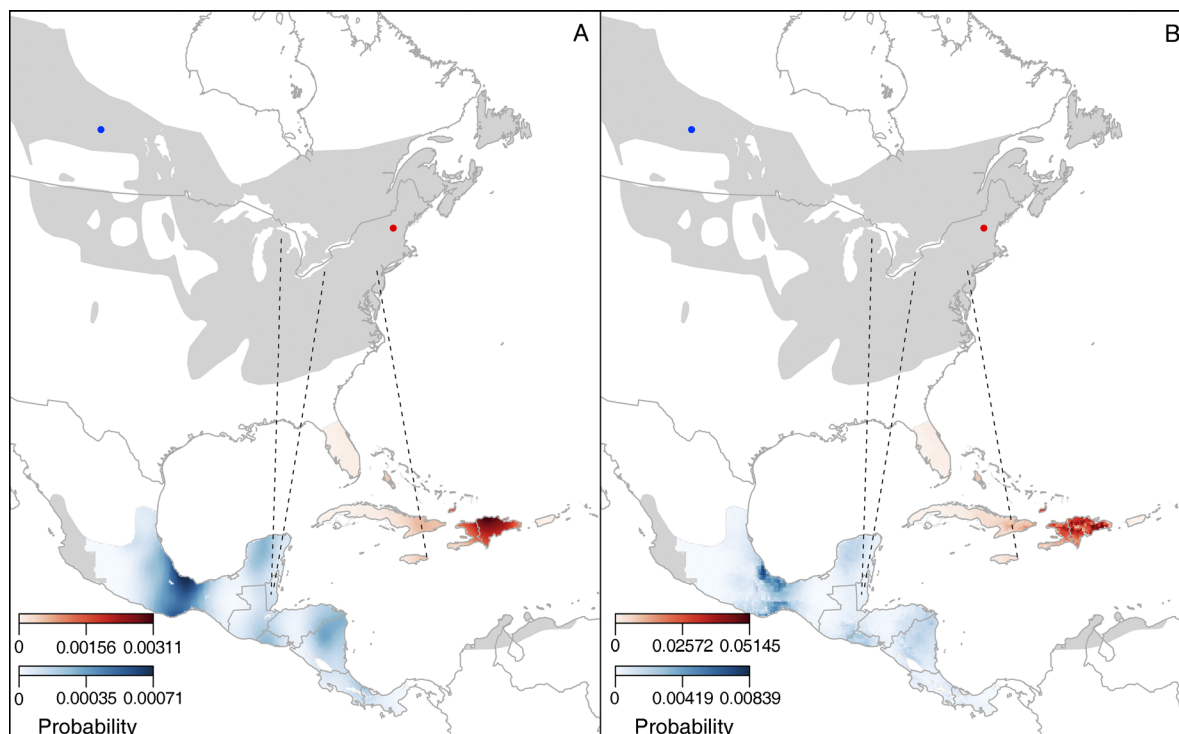
Fig. 3. Ovenbirds captured during the breeding season exhibited nonoverlapping nonbreeding distributions between east and west populations, which were supported by three band encounters (gray dotted lines connecting the location of original capture and the location where the individual was recaptured; see *Methods* for selection criteria). Ovenbirds breeding in Saskatchewan, Canada (blue dot) spent the nonbreeding season in Central America with the highest probability of origin (blue color ramp) found in southern Mexico. Geolocators recovered from New Hampshire, USA (red dot) indicate Ovenbirds wintered exclusively in the Caribbean with the highest probability of origin found on the island of Hispaniola (red color gradient). Darker colors indicate a higher probability of origin for a specific breeding location. The probability of origin was calculated using geolocator estimates from all geolocators recovered from a single capture location (panel A) and Ovenbird abundance derived using eBird data (panel B). Both breeding and nonbreeding distributions of Ovenbirds are shown in light gray.

different nonbreeding areas (Heckscher et al. 2011, Delmore et al. 2012). However, our findings suggest that the nonbreeding locations of birds breeding along the Atlantic coast are more similar to each other than to birds breeding in the western portion of their distribution. These findings suggest that changes in ecological conditions or habitat within the Caribbean and Central America could impact Ovenbirds differently in the eastern or western portions of their distribution, respectively. Further research is needed to identify more subtle patterns of connectivity within each of these regions as well as the underlying mechanisms causing the divide between eastern and western populations.

Leap-frog migration, where populations breeding at northerly locations migrate to areas in the nonbreeding distribution that are south of more southerly breeding populations (Newton 2008), is common among shorebirds (Alerstam and Högstedt 1980) and has been demonstrated in migratory songbirds with the use of hydrogen-stable isotopes (Langin et al. 2009). Here, we found the highest posterior probability of origin during the breeding season for individuals captured in Everglades National Park, Florida, USA was further south

TABLE 1. Values used to scale the strength of migratory connectivity.

Capture location	n	$1/n$	Location error	Scaled migratory connectivity
Breeding season				
HBEF	21	0.0476	0.7830	0.525
Canada	8	0.1250	0.8580	0.213
Nonbreeding season				
Everglades	3	0.3333	0.9344	0.360
Jamaica	9	0.1111	0.7741	0.635
Puerto Rico	4	0.2500	0.9875	0.336

Notes: Parameters are the number of geolocators captured at each location (n), the expected posterior probability of origin if there was no overlap of individuals during subsequent seasons ($1/n$), and the maximum posterior probability of origin at a known capture location (location error). In theory, the maximum posterior probability of origin should be equal to 1, however because of the uncertainty associated with geolocator estimates, the maximum posterior probability of origin was less than 1. The strength of connectivity was scaled (see *Methods*) using the values in the table. HBEF stands for Hubbard Brook Experimental Forest.

compared to individuals captured in Jamaica. However, due to the mainly east-west spatial distribution of the Greater Antillean islands, and the degree of overlap in the probability of origin for the capture locations located within the Caribbean, we cannot say conclusively whether or not Ovenbirds exhibit leap-frog migration.

Statistical techniques that reduce and incorporate the uncertainty in location estimates derived using archival light-level geolocators are needed to refine our understanding of migratory connectivity for migratory populations (Bridge et al. 2013). As has been used previously in studies based on assignments using stable isotopes (Royle and Rubenstein 2004, Wunder and Norris 2008, González-Prieto et al. 2011, Flockhart et al. 2013, Hallworth et al. 2013) we incorporated Ovenbird abundance, which assumes the probability of origin to be affected only by the population abundance during the breeding or nonbreeding season, into location estimates using Bayes' rule to reduce the potential area of origin generated by geolocator estimates alone. Incorporating prior probabilities based upon bird abundance into posterior probability of origin estimates reduced the potential area of origin during both the breeding (90.37% ± 1.05%) and nonbreeding (62.30% ± 1.69%) seasons. Using abundance estimates in conjunction with geolocator data could help identify areas of special concern or where to focus conservation efforts for species of concern. Here, we relied on Breeding Bird Survey data (Sauer et al. 2012) and eBird checklists submitted by citizen scientists to create abundance maps during breeding and nonbreeding seasons, respectively. To date, eBird checklists within the nonbreeding distribution of many Neotropical migrants are concentrated in highly travelled areas (e.g., Costa Rica) and lacking in locations with limited accessibility (e.g., Cuba, high elevations [Snäll et al. 2011]), which may encompass large areas of a species' distribution. Thus, using abundance estimates derived using eBird checklists may only be useful for species with large distributions. Observer differences and species detection may also limit the use of eBird data for species difficult to identify and/or are cryptic. In addition, common species may not be reported or get overlooked (Snäll et al. 2011) adding to the uncertainty in the estimates for common species. Despite the limitations mentioned above, eBird data are the only range-wide abundance data available for migratory birds during the nonbreeding season (Figs. 3 and 4).

Our findings suggest that the strength of migratory connectivity depends upon on the spatial scale of interest. We found strong overall migratory connectivity at broad spatial scales but weaker patterns within subpopulations, although some locations, particularly Jamaica and New Hampshire, exhibited moderate connectivity. Our measure of connectivity was corrected for the number of individuals captured; however, our power to assess the degree of connectivity may increase if our sample size was larger. Our assessment of connectivity may be biased by the amount of land area in different portions of the nonbreeding season, with strong connectivity in areas with limited land area (i.e., Caribbean) and weak connectivity in areas with large land masses (i.e., Central America). In addition, the uncertainty in geolocator estimates increases toward the equator potentially leading to weak connectivity estimates for populations captured during the breeding season. However, geolocators were deployed during the breeding season for one of the two populations that exhibited moderate connectivity (HBEF) and Ovenbirds from all capture locations spent the nonbreeding season at approximately the same latitude (Fig. 3) minimizing the influence of uncertainty in geolocator estimates between capture locations.

Probability of origin maps could be used to focus conservation efforts as well as predict the influence of disturbances on specific populations. Our findings suggest that the breeding population at Hubbard Brook Experimental Forest in New Hampshire, USA, could be impacted by events, such as large disturbances like hurricanes on the island of Hispaniola. Similarly, large-scale disturbance in Jamaica will likely impact Ovenbirds breeding in the northeastern United States. In contrast, locations such as Puerto Rico that exhibit weak connectivity would likely be unaffected by localized pressures during the breeding season as individuals originate from a wider array of breeding locations.

We were able to identify the strength of migratory connectivity at a broad spatial scale with the use of archival light-level geolocators deployed at multiple locations within the Ovenbirds' distribution. Understanding how the strength of migratory connectivity impacts life history strategies, population dynamics, seasonal interactions and a populations' response to selective pressures, requires an understanding of migratory connectivity at both broad and local spatial scales. Currently, the uncertainty associated with geolocator estimates precludes their use for determining local-scale connectivity information. In an attempt to reduce the uncertainty of geolocator estimates and provide more detailed location information we refined the geolocator estimates using bird abundance. In addition, we created probabilistic origin maps and identified migration routes between subsequent seasons, which are critical for assessing how populations respond to things such as habitat alteration, weather events and climate change throughout their range. Although our findings have improved our understanding of migratory connectivity for the Ovenbird, further research is needed to determine (1) the utility of using eBird data to provide abundance estimates of Neotropical migrants during the nonbreeding season, and (2) additional sampling locations are needed to locate where the divide between eastern and western populations of Ovenbirds occurs and identify the underlying mechanisms for the divide.
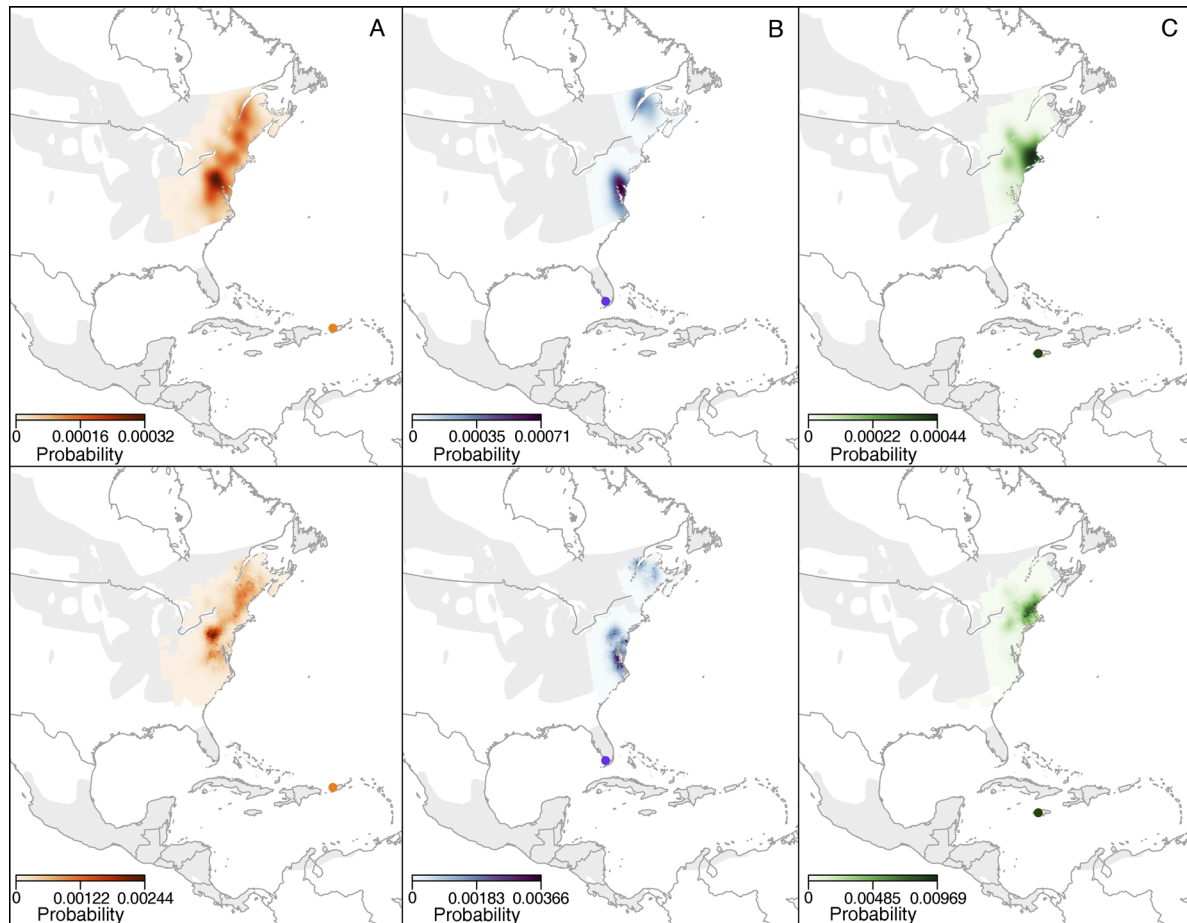
Fig. 4. Ovenbirds captured during the nonbreeding season had overlapping breeding locations. Ovenbirds wintering in Puerto Rico (orange dot, panel A) exhibited weak connectivity and bred along the entirety of the Atlantic coast with the highest probability of origin located along the mid-Atlantic region. Similarly, Ovenbirds wintering in Everglades National Park (blue dot, panel B) exhibited weak connectivity with the highest probability of origin in the mid-Atlantic region. Conversely, Ovenbirds captured in Jamaica (green dot, panel C) exhibited moderate connectivity with the highest probability of origin found in northeastern United States. Darker colors indicate a higher probability of origin for a specific wintering location (see Fig. 2 legend). The probability of origin was calculated using geolocator estimates from all geolocators recovered from a single capture location (top panel) and the posterior probability of origin when incorporating Ovenbird abundance obtained from the Breeding Bird Survey (Sauer et al. 2012, bottom panel) as a prior probability using Bayes' rule. Both breeding and nonbreeding distributions of Ovenbirds are shown in light gray.

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SUPPLEMENTAL MATERIAL

Ecological Archives

The Appendix is available online: http://dx.doi.org/10.1890/14-0195.1.sm

Data Availability

Data associated with this paper have been deposited at the Smithsonian Migratory Bird Center: http://dx.doi.org/10.5479/data.smbc.20140815